

Birds have primate-like numbers of neurons in the forebrain

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Some birds achieve primate-like levels of cognition, even though their brains tend to be much smaller in absolute size. This poses a fundamental problem in comparative and computational neuroscience, because small brains are expected to have a lower information-processing capacity. Using the isotropic fractionator to determine numbers of neurons in specific brain regions, here we show that the brains of parrots and songbirds contain on average twice as many neurons as primate brains of the same mass, indicating that avian brains have higher neuron packing densities than mammalian brains. Additionally, corvids and parrots have much higher proportions of brain neurons located in the pallial telencephalon compared with primates or other mammals and birds. Thus, large-brained parrots and corvids have forebrain neuron counts equal to or greater than primates with much larger brains. We suggest that the large numbers of neurons concentrated in high densities in the telencephalon substantially contribute to the neural basis of avian intelligence.

intelligence | evolution | brain size | number of neurons | birds

M any birds have cognitive abilities that match or surpass those of mammals (1). Corvids and parrots appear to be cognitively superior to other birds, rivalling great apes in many psychological domains (1–3). They manufacture and use tools (4, 5), solve problems insightfully (6), make inferences about causal mechanisms (7), recognize themselves in a mirror (8), plan for future needs (9), and use their own experience to anticipate future behavior of conspecifics (10) or even humans (11), to mention just a few striking abilities. In addition, parrots and songbirds (including corvids) share with humans and a few other animal groups a rare capacity for vocal learning (12), and parrots can learn words and use them to communicate with humans (13).

Superficially, the architecture of the avian brain appears very different from that of mammals, but recent work demonstrates that, despite a lack of layered neocortex, large areas of the avian forebrain are homologous to mammalian cortex (14-16), conform to the same organizational principles (15, 17, 18), and play similar roles in higher cognitive functions (14, 19), including executive control (20, 21). However, bird brains are small and the computational mechanisms enabling corvids and parrots to achieve ape-like intelligence with much smaller brains remain unclear. The notion that higher encephalization (relative brain size deviation from brain-body allometry) endows species with improved cognitive abilities has recently been challenged by data suggesting that intelligence instead depends on the absolute number of cerebral neurons and their connections (22-25). This is in line with recent findings that absolute rather than relative brain size is the best predictor of cognitive capacity (26-28). However, although corvids and parrots feature encephalization comparable to that of monkeys and apes, their absolute brain size remains small (29, 30). The largest average brain size in corvids and parrots does not exceed 15.4 g found in the common raven (29) and 24.7 g found in the hyacinth macaw (30), respectively. Do corvids and parrots provide a strong case for reviving encephalization as a valid measure of brain functional

capacity? Not necessarily: it has recently been discovered that the relationship between brain mass and number of brain neurons differs starkly between mammalian clades (31). Avian brains seem to consist of small, tightly packed neurons, and it is thus possible that they can accommodate numbers of neurons that are comparable to those found in the much larger primate brains. However, to date, no quantitative data have been available to test this hypothesis.

Here, we analyze how numbers of neurons compare across birds and mammals (32-39) of equivalent brain mass, and determine the cellular scaling rules for brains of songbirds and parrots. Using the isotropic fractionator (40), we estimated the total numbers of neuronal and nonneuronal cells in the cerebral hemispheres, cerebellum, diencephalon, tectum, and brainstem in a sample of 11 parrot species, 13 vocal learning songbird species (including 6 corvids), and 4 additional model species representing other avian clades (Figs. S1 and S2). Because most of the cited mammalian studies analyzed cellular composition of only three brain subdivisions, namely the pallium (referred to as the cerebral cortex in those papers), the cerebellum, and rest of brain, we divided the avian brain identically to ensure an accurate comparison of neuronal numbers, densities, and relative distribution of neurons in birds and mammals. Specifically, the avian pallium (comprising the hyperpallium, mesopallium, nidopallium, arcopallium, and hippocampus) was compared with its homolog-the mammalian pallium (comprising the neocortex, hippocampus, olfactory cortices such as piriform and entorhinal cortex, and pallial

Significance

Birds are remarkably intelligent, although their brains are small. Corvids and some parrots are capable of cognitive feats comparable to those of great apes. How do birds achieve impressive cognitive prowess with walnut-sized brains? We investigated the cellular composition of the brains of 28 avian species, uncovering a straightforward solution to the puzzle: brains of songbirds and parrots contain very large numbers of neurons, at neuronal densities considerably exceeding those found in mammals. Because these "extra" neurons are predominantly located in the forebrain, large parrots and corvids have the same or greater forebrain neuron counts as monkeys with much larger brains. Avian brains thus have the potential to provide much higher "cognitive power" per unit mass than do mammalian brains.

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Fig. 1. Cellular scaling rules for brains of songbirds and parrots compared with those for mammals. (A) Avian and mammalian brains depicted at the same scale. Numbers under each brain represent brain mass (in grams) and total number of brain neurons (in millions). Notice that brains of songbirds (goldcrest, starling, and rook) and parrots (cockatoo) contain more than twice as many neurons as rodent (mouse and rat) and primate (marmoset and galago) brains of similar size. (Scale bar: 10 mm.) (B) Brain mass plotted as a function of total number of neurons. Note that allometric lines for songbirds (green line) and parrots (red line) do not differ from each other, but they do differ from allometric lines for mammals (for statistics, see SI Results). (C) Brain mass plotted as a function of total number of nonneuronal cells. (D) Brain mass plotted as a function of body mass. (E) Total number of brain neurons plotted as a function of body mass. Allometric lines for the taxa examined are significantly different (for statistics, see SI Results). Each point represents the average values for one species. Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. The fitted lines represent reduced major axis (RMA) regressions and are shown only for correlations that are significant [coefficient of determination (r^2) ranges between 0.831 and 0.997; $P \le 0.021$ in all cases]. Because nonneuronal scaling rules are very similar across the clades analyzed, the regression lines are omitted in C. Data for mammals are from published reports (for details, see Methods). CL, pigeon (Columba livia); DN, emu (Dromaius novaehollandiae); GG, red junglefowl (Gallus gallus); TA, barn owl (Tyto alba).

amygdala) (14–16, 41). The avian subpallium (formed by the striatum, pallidum, and septum), diencephalon, tectum, and brainstem were pooled and compared with the same regions of mammalian brains that are referred to as "the rest of brain." The cerebellum is directly compared between the two clades. The results of our study reveal that avian brains contain many more pallial neurons than equivalently sized mammalian brains.

Results

Total Numbers of Neurons. We found that the bird brains have more neurons than mammalian brains and even primate brains of similar mass (Fig. 1 A and B), and have very high neuronal densities (Fig. 2 B and C). Among the songbirds studied, weighing between 4.5 and 1,070 g, brain mass ranges from 0.36 to 14.13 g, and total numbers of neurons in the brain from 136 million to 2.17 billion (Fig. S3 and Table S1; for complete data see Datasets S1 and S2). In the parrots studied, body mass ranges between 23 and 1,008 g, brain mass from 1.15 to 20.73 g, and numbers of brain neurons from 227 million to 3.14 billion. Interestingly, the relationship between brain mass and the number of brain neurons can be described by similar power functions in these two bird



Songbirds, Parrots, Pigeon (CL), Red junglefowl (GG), Barn owl (TA), Emu (DN).

Fig. 2. Cellular densities in avian brains. (A) Lateral view of the starling brain showing the brain regions analyzed (for details, see *SI Methods* and Fig. S2). Neuronal (*B* and *C*) and nonneuronal cell density (*D* and *E*) plotted as a function of brain mass. Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. All graphs are plotted using the same *y*-axis scale for comparison. Note that neuronal density varies greatly among principal brain divisions and decreases significantly with increasing brain mass in all divisions but the telencephalon, whereas nonneuronal cell density is similar across brain divisions and species, but lower in the telencephalon (for statistics, see *SI Results*). The fitted lines represent RMA regressions and are shown only for correlations that are significant (*r*² ranges between 0.410 and 0.962; *P* ≤ 0.030 in all cases).



Fig. 3. Neuronal densities and relative distribution of neurons in birds and mammals. (A-C) Neuronal densities in the pallium (A), cerebellum (B), and rest of the brain (C). Note that neuronal densities are higher in parrots and songbirds than in mammals (for statistics, see SI Results). (D-F) Average proportions of neurons contained in the pallium (D), cerebellum (E), and rest of the brain (F). Note that increasing proportions of brain neurons in the rest of the brain in parrots are attributable specifically to increasing numbers of neurons in the subpallium (Fig. 5). Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. The fitted lines represent RMA regressions and are shown only for correlations that are significant (r^2 ranges between 0.389 and 0.956; $P \leq$ 0.033 in all cases). (G) Brains of corvids (jay and raven), parrots (macaw), and primates (monkeys) are drawn at the same scale. Numbers under each brain represent mass of the pallium (in grams) and total numbers of pallial/cortical neurons (in millions). Circular graphs show proportions of neurons contained in the pallium (green), cerebellum (red), and rest of the brain (yellow). Notice that brains of these highly intelligent birds harbor absolute numbers of neurons that are comparable, or even larger than those of primates with much larger brains. (Scale bar: 10 mm.) Data for mammals are from published reports (for details, see Methods). CL, pigeon; DN, emu; GG, red junglefowl; TA, barn owl.

groups (Table S2). Thus, songbirds and parrots with similar brain masses also have similar total numbers of brain neurons, as shown in Fig. 1B. Because the scaling exponents are significantly higher than 1.0 in both groups, any gain in number of brain neurons is accompanied by an even more pronounced gain of mass: a 10fold increase in the number of neurons results in a 16.9- and 14.0-fold larger brain in songbirds and parrots, respectively. With their higher neuronal densities (Fig. 3A-C), songbird and parrot brains accommodate about twice as many neurons as primate brains of the same mass and two to four times more neurons than rodent brains of equivalent mass (Fig. 1B). Songbirds and parrots also show a large brain mass for their body mass compared with nonprimate mammals (Fig. S4 A and B). Consequently, they have many more neurons than a nonprimate mammal of the same body size (Fig. 1E). For instance, the goldcrest's body mass is ~9-fold smaller than the mouse, but its brain has ~2.3-fold more neurons. Large corvids and parrots possess the largest avian brains, harboring the highest absolute numbers of neurons (Fig. 1 D and E and Fig. S4C). Their total numbers of neurons are comparable to those of small monkeys or much larger ungulates (Fig. S5).

Relative Distribution of Mass and Neurons. The bird/mammal comparison becomes even more striking when the relative distribution of neurons among the major brain components is taken into consideration. In the birds examined, the telencephalon mass fraction increases with brain size at the expense of all other brain components, ranging from 63% to 80% in songbirds, and from 71% to 85% in parrots (Fig. 4 *A* and *B* and Table S3); the relative proportion of the telencephalon resembles that reported for primates (42) (primates, 74 ± 5%; songbirds, 72 ± 6%; parrots, 78 ± 5%). The cerebellar mass fraction decreases from 11% to 8% in songbirds, and from 11% to 6% in parrots. Besides this, telencephalon mass scales approximately isometrically with the number of neurons, whereas all other brain components hyperscale in mass as they gain neurons (Table S2), because neuronal densities decrease and average neuronal sizes increase significantly as brains get larger within all brain parts but the telencephalon (Fig. 2 B and C). Thus, in contrast to mammals, larger brains of songbirds and parrots contain increasing proportions of neurons in the telencephalon, and correspondingly decreasing proportions of brain neurons in the cerebellum and other brain regions (Fig. 4 C and D). Neuronal densities in the avian pallium exceed those observed in the primate pallium by a factor of 3-4 (Fig. 3A). Hence, the telencephalon houses 38-62% of all brain neurons in songbirds and 53-78% in parrots (Fig. 4C); the pallium houses 33-55% in songbirds and 46-61% in parrots (Fig. 3D and Table S4). This markedly contrasts with the situation found in mammals, in which the pallium accounts for most of total brain volume, but the cerebellum houses a large majority of brain neurons (32-39) (Fig. 3 D-F). Notably, the human pallium contains a mere 19% of brain neurons but represents 82% of brain mass (38). Thus, when avian and mammalian brains of equivalent size are compared, avian pallial neurons greatly outnumber those observed in the mammalian pallium (Fig. 3G and Fig. S5). For instance, the goldcrest has ~64 million pallial neurons, almost five times more than the mouse pallium. The raven or the kea have ~ 1.2 billion pallial neurons, more than in the pallium of a capuchin monkey, and the blue-and-yellow macaw has ~1.9 billion pallial neurons, more than in the pallium of a rhesus monkey.

Subpallium. Although once believed to constitute almost the entire avian telencephalon (14), the subpallium (basal ganglia homolog) accounts only for 10-22% of total telencephalon volume in songbirds and for 15-18% in parrots, and houses only 9-16% of telencephalic neurons in songbirds and 14-24% in parrots (Tables S3 and S4). In songbirds, both the relative mass of the subpallium and the fraction of telencephalic



Fig. 4. Relative distribution of mass and cells in avian brains. Average percentages of mass (*A* and *B*), number of neurons (*C* and *D*), and number of nonneuronal cells (*E* and *F*) contained in the principal brain divisions relative to the whole brain in each species, plotted against brain mass. Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. The fitted lines represent RMA regressions and are shown only for correlations that are significant (r^2 ranges between 0.389 and 0.956; $P \le 0.023$ in all case). Note that both telencephalon mass fraction and proportions of neuronal and nonneuronal cells contained in the telencephalon increase with brain size.

neurons contained within it decrease with increasing telencephalon size (Fig. 5 *B* and *C*). In parrots, in contrast, the relative mass remains constant and neuronal fraction increases with telencephalon size. Therefore, large-brained parrots have a relatively larger subpallium within the telencephalon that accommodates relatively more telencephalic neurons than that of large-brained songbirds (Fig. 5 *B–D*), implying that parrots have evolved a specific, previously unrecognized cerebrotype (43) distinguished by a higher number of neurons allocated to the subpallium. Because subpallial structures play an important role in sensory and motor learning and execution of motor behavior (15, 44), we suggest that the relatively enlarged subpallium in large parrots is likely associated with their greater learning skills, including vocal learning, and enhanced foot and beak dexterity (5, 6, 13, 45). **Nonneuronal Scaling Rules.** Although neuronal scaling rules for avian brains differ from those for mammalian brains (Fig. 1*B*), nonneuronal scaling rules are shared between the two vertebrate classes (Fig. 1*C* and Table S2). In line with data from all mammals analyzed so far (32–39), the densities of nonneuronal (glial and endothelial) cells remain similar across bird species in all brain structures, except for the telencephalon, where nonneuronal cell density appears to be distinctively lower (Fig. 2 *D* and *E*). The latter may be a specific avian feature, as it has not been observed in mammals (31).

Glia/Neuron Ratio. Neurons outnumber nonneuronal cells in both bird groups examined (Fig. S64 and Table S5). The proportion of nonneuronal cells in the brain ranges between 21% and 37% in songbirds and from 31% to 41% in parrots. Hence, the maximal glia/neuron ratio (if all nonneuronal cells were glial cells) for the whole brain ranges from 0.27 to 0.59 in songbirds and from 0.44 to 0.69 in parrots. Like in mammals (32-39, 46), the proportion of nonneuronal cells is very small in the cerebellum, varying between 12% and 19% in songbirds and between 14% and 19% in parrots, but, in contrast to mammals, nonneuronal cells also constitute a minor cellular fraction in the telencephalon, representing 21-40% of cells in songbirds and 31-43% of cells in parrots (Fig. S6B). Nonneuronal cells predominate in the remaining brain regions analyzed, representing in songbirds and parrots, respectively, 60-90% and 79–94% of all cells in the diencephalon, 28–70% and 52-71% of all cells in the tectum, and 76-95% and 85-95% of all cells in the brainstem (Fig. S6B). The fact that neurons constitute an extremely small cellular fraction in the diencephalon of many avian species is an unexpected finding. Given that nonneuronal cell densities are similar to those found in most other brain divisions investigated (Fig. 2D and E), this is unlikely to be due to a technical error. The numeric preponderance of neurons over nonneuronal cells in the bird brain as a whole is therefore due to the disproportionately large numbers of neurons in the telencephalon and cerebellum.

Corvid Brain as a Scaled-Up Songbird Brain. When considering the numbers of neurons and nonneuronal cells and their allocations to the major brain divisions, the same scaling rules apply to the brains of corvids and noncorvid songbirds (Figs. 1–5 and Table S2). Thus, it is not cellular composition but encephalization that sets corvids apart from other songbirds. Technically, residual brain mass calculated from regressions for all songbirds [species examined in this study: $t_{(2,11)} = 2.542$, P = 0.03, Fig. 1D; species collated from literature: $t_{(2,848)} = 7.55$, $P < 10^{-6}$, Fig. S4C]. Because corvid brains tend to be larger than brains of noncorvid songbirds for any given body size (Fig. 1D and Fig. S4C), corvids have larger total numbers of neurons than noncorvid songbirds of the same body size (Fig. 1E). We suggest that corvid brains are scaled-up songbird brains, just as humans brains are to brains of nonhuman primates (38, 47), and that large absolute numbers of neurons endow corvids with superior cognitive abilities.

Comparison with Other Birds. The similarity of neuronal scaling rules between songbirds and parrots is not too surprising, considering their close phylogenetic relationship (48–51). The examination of outgroup taxa, however, suggests that, as in mammals (31), different neuronal scaling rules apply to various bird lineages. The closest relative to songbirds and parrots of the species sampled, the barn owl (Fig. S1) (48–51) resembles songbirds and parrots in terms of encephalization (Fig. 1D), relative telencephalon size (Fig. 4A), and neuronal densities in the telencephalon and diencephalon (Fig. 2C), but has a proportionally smaller subpallium (Fig. 5B) and lower neuronal densities in the tectum and cerebellum (Fig. 2C). The emu, the red junglefowl, and the pigeon, all species representing more basal bird lineages (Fig. S1), share lower degree of encephalization (Fig. 1D), a proportionally smaller telencephalon (Fig. 4A), small telencephalic and dominant cerebellar neuronal fractions (Fig. 4C), generally lower neuronal densities (Fig. 2C), and larger glia/neuron ratios (Fig. S6).



Fig. 5. Subpallium in avian telencephalon. (*A*) Diagram of sagittal section through the zebra finch brain showing relative position and size of the pallium and subpallium. (*B* and *C*) Average percentages of mass (*B*), number of neurons (*C*) contained in the subpallium relative to the whole telencephalon in each species, plotted against telencephalon mass. (*D*) Relationship between numbers of subpallial and pallial neurons. Note that, in parrots, the number of neurons in the subpallium increases faster than in the pallium (scaling exponent = 1.19 ± 0.13), whereas an opposite trend is observed in songbirds (scaling exponent = 0.91 ± 0.1). The fitted lines represent RMA regressions and are shown only for correlations that are significant (r^2 ranges between 0.379 and 0.981; $P \le 0.025$ in all cases). Songbirds shown in green (data points representing noncorvids are light green, and data points representing corvids are dark green), parrots in red, and other birds in black. CL, pigeon; DN, emu; GG, red junglefowl; TA, barn owl.

Therefore, their brains harbor much smaller absolute numbers of neurons than brains of equivalently sized songbirds or parrots. For instance, although a red junglefowl is \sim 50-fold heavier than a great tit, both birds have approximately the same number of brain neurons (Fig. 1*E* and Fig. S3). Remarkably, even in these basal birds, neuronal densities in the pallium are still comparable to those observed in the primate cortex (Fig. 3*A*). Thus, high neuronal density in the telencephalon appears characteristic of all birds. This means that neuronal densities in the primate pallium are matched by those of chicken and emu, but surpassed by those of songbirds and parrots.

Discussion

Assuming that brains of parrots and songbirds have diverged from the presumptive ancestral avian pattern found in all representatives of basal bird lineages examined and characterized by a mammal-like numerical preponderance of cerebellar neurons, we suggest that birds generally have higher neuronal densities than mammals, and further that parrots and songbirds have acquired an expanded telencephalon with increased neuronal densities. Two proximate, synergistic mechanisms likely contributed to this evolutionary process. First, just like the expansion of neocortex in primates (52), the expansion of the telencephalon in parrots and songbirds is associated with delayed and protracted neurogenesis, an expanded subventricular zone, and delayed neuronal maturation (53-55). It has been suggested that extensive posthatching neurogenesis and brain maturation promote learning from conspecifics and may have facilitated the emergence of specialized circuits that mediate vocal learning and possibly also other flexible and innovative behaviors (56). Second, analyses of brain gene expression profiles strongly suggest that songbirds and parrots independently evolved vocal learning pathways by duplication of preexisting, surrounding motor circuits (57, 58). Intriguingly, parrot pallial song nuclei underwent a further duplication event to evolve a unique additional circuit, the so-called shell song system, which seems to be particularly well developed in large-brained parrots (45). What ultimate mechanisms drive the evolution of the enlarged, neuron-rich telencephalon, which sets parrots and songbirds apart from the more basal birds we examined, remains poorly understood. We suggest that this expansion has been due to simultaneous selective pressures on cognitive enhancement and an evolutionary constraint on brain size, which may stem from the constraints on body size imposed by active flight. Altriciality and the extended parental care that has developed in avian ancestors simultaneously relaxed constraints on the duration of ontogenesis, a precondition for telencephalic expansion by the mechanisms described above (56). Moreover, a short neck relative to many other bird lineages may have reduced biophysical constraints on head size (cf. ref. 59).

Our finding of greater than primate-like numbers of neurons in the pallium of parrots and songbirds suggests that the large absolute numbers of telencephalic neurons in these two clades provide a means of increasing computational capacity, supporting their advanced behavioral and cognitive complexity, despite their physically smaller brains. Moreover, a short interneuronal distance, the corollary of the extremely high packing densities of their telencephalic neurons, likely results in a high speed of information processing, which may further enhance cognitive abilities of these birds. Thus, the nuclear architecture of the avian brain appears to exhibit more efficient packing of neurons and their interconnections than the layered architecture of the mammalian neocortex.

Further comparative studies on additional species are required to determine whether the high neuronal densities and preferential allocation of neurons to the telencephalon represent unique features of songbirds, parrots, and perhaps some other clades like owls, or have evolved multiple times independently in large-brained birds. More detailed quantitative studies should assess the distribution of neurons among various telencephalic regions involved in specific circuits subserving specific functions. The results, combined with behavioral studies, will enable us to determine the causal relationships between neuronal numbers and densities and perceptual, cognitive, and executive/motor abilities, and greatly advance our understanding of potential mechanisms linking neuronal density with information-processing capacity.

Methods

Experimental procedures were all approved by the Institutional Animal Care and Use Committee at Charles University in Prague. Altogether, 73 birds belonging to 28 species were used in this study (Table S1). Animals were killed by an overdose of halothane and perfused with 4% (wt/wt) paraformaldehyde. Brains were removed, postfixed for an additional 7-21 d, and dissected into the cerebral hemispheres, cerebellum, diencephalon, tectum, and brainstem. In one individual per species, one hemisphere was dissected into the pallium and the subpallium. In these brain components, the total numbers of cells, neurons, and nonneuronal cells were estimated following the procedure of isotropic fractionation described earlier (40). The reduced major axis regressions to power functions were calculated to describe how structure mass, numbers of cells, and densities are interrelated across species. Analysis of covariance was used to compare scaling among groups (taxonomic orders or brain regions). To compare relative brain size between corvid and noncorvid songbirds, we computed t test on the residuals of a log-log regression of brain mass against body mass (residual brain mass, hereafter). For the comparison with cellular scaling rules reported previously for mammals, the reduced major axis regressions were calculated from quantitative data published for primates (33, 37, 38), rodents excluding the naked mole-rat (32, 39), and artiodactyls (36). In addition, the published quantitative data for Eulipothyphla (34) and Afrotheria (35) were used for comparison in Fig. S5. Further details are provided in Supporting Information.

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Supporting Information

Olkowicz et al. 10.1073/pnas.1517131113

SI Methods

Animals. Three individuals per species were collected with some exceptions for large parrots, two songbird species, and the emu, in which only one or two birds were examined. The following species were purchased from local breeders: all species of parrots, zebra finch, azure-winged magpie, common hill myna, raven, emu, red junglefowl, and barn owl. According to some authors, the genetic integrity of the red junglefowl Gallus gallus is endangered due to hybridization with domestic or feral chickens at the edge of fragmented forests (60). Although we thus cannot exclude admixture of genes from domestic or feral chicken, the red junglefowl used in this study appeared to have a pure wild phenotype. The remaining birds were wild-caught in Czech Republic (Permission No. 00212/CS/2013 and 446/2013). All birds were sexually mature or at least had adult-like size and plumage coloration. We determined the sex of all animals upon dissection and found that we had included both males and females in the analysis. The sample sizes were too small to analyze sex differences.

Animals were killed by an overdose of halothane. They were weighed and immediately perfused transcardially with warmed PBS containing 0.1% heparin followed by cold phosphate-buffered 4% (wt/wt) paraformaldehyde solution. Skulls were partially opened and postfixed for 30–60 min, after which brains were dissected and weighed. Brains were postfixed for additional 7–21 d and then dissected. All procedures were approved by Institutional Animal Care and Use Committee at Charles University in Prague, Ministry of Culture (Permission No. 47987/2013) and Ministry of the Environment of the Czech Republic (Permission No. 53404/ENV/13-2299/630/13).

Dissection. Brains were dissected into distinct components using the Olympus SZX 16 stereomicroscope. The cerebral hemispheres were detached from the diencephalon by a straight cut separating the subpallium from the thalamus. The tectum (optic lobe) was bilaterally excised from the surface of the brainstem. The excised parts included most of the tectal gray, optic tectum, and torus semicircularis. Both left and right tectum were processed together. The cerebellum was cut off at the surface of the brainstem. Finally, the remaining structures were dissected into diencephalon (rostral part) and brainstem (caudal part) along the plane connecting the posterior commissure dorsally and hypothalamus-mesencephalon boundary ventrally. For most individuals, only one cerebral hemisphere was processed, because in our preliminary studies we detected negligible differences between left and right hemisphere mass and cell numbers. In one individual per species, the second hemisphere was dissected into the pallium and the subpallium. These hemispheres were embedded in agarose and sectioned on a vibratome at 300-500 µm (depending on size of a hemisphere) in the coronal plane. Under oblique transmitted light at the stereomicroscope and with the use of a microsurgical knife (Stab Knife Straight; 5.5 mm; REF 7516; Surgical Specialties Corporation), we manually dissected the pallium from subpallium on each section by cutting along the pallial-subpallial lamina, as defined by Reiner et al. (41). The subpallium included all major subpallial cell groups enumerated therein; the remaining parts of the telencephalon constituted the pallium. The dissected structures were dried with paper towel, weighed, incubated in 30% (wt/wt) sucrose solution until they sank, then transferred into antifreeze (30% glycerol, 30% ethylene glycol, 40% phosphate buffer), and frozen for further processing.

rons, and nonneuronal cells following the procedure of isotropic fractionation described earlier (40). Briefly, each dissected brain division was homogenized in 40 mM sodium citrate with 1% Triton X-100 using Tenbroeck tissue grinders (Wheaton). When turned into an isotropic suspension of isolated cell nuclei, homogenates were stained with the florescent DNA marker DAPI, adjusted to a defined volume, and kept homogenous by agitation. The total number of nuclei in suspension, and therefore the total number of cells in original tissue, was estimated by determining density of nuclei in small fractions drawn from a homogenate. At least four 10-µL aliquots were sampled and counted using a Neubauer improved counting chamber (BDH; Dagenham) with an Olympus BX51 microscope equipped with epifluorescence and appropriate filter settings (Olympus filters U-MWU2 for DAPI and U-MWG2 for Alexa Fluor 546-conjugated secondary antibodies); additional aliquots (typically two to five) were assessed when needed to reach the coefficient of variation among counts ≤ 0.15 . Once the total cell number was known, the proportion of neurons was determined by immunocytochemical detection of neuronal nuclear marker NeuN (61). This neuronspecific protein was detected by the mouse monoclonal antibody anti-NeuN (clone A60; Chemicon; dilution, 1:800), which was recently characterized by Western blotting with chick brain samples and shown to react with a protein of the same molecular weight as in mammals (62), indicating that it does not cross-react with other proteins in birds. The binding sites of the primary antibody were revealed by Alexa Fluor 546-conjugated goat antimouse IgG (Life Technologies; dilution, 1:500). An electronic hematologic counter (Alchem Grupa) was used to count simultaneously DAPI-labeled and NeuN-immunopositive nuclei in the Neubauer chamber. A minimum of 500 nuclei was counted to estimate percentage of double-labeled neuronal nuclei. Numbers of nonneuronal cells were derived by subtraction.

Isotropic Fractionator. We estimated total numbers of cells, neu-

Data Analysis. All analyses were performed using average values for each species; variables were log-transformed before the subsequent statistical analyses. Correlations between variables were assessed using nonparametric Spearman rank test. If a significance criterion of P < 0.05 was reached, the reduced major axis regressions were calculated to describe how structure mass, numbers of cells, and densities are interrelated across species. Analysis of covariance (ANCOVA) was used to compare scaling among groups (taxonomic orders or brain regions). The significant interaction between categorical and continuous predictors in the full-factorial ANCOVA demonstrates statistically different slopes of the regression lines among groups and precludes the direct comparison of the magnitude of differences among groups based just on the differences in intercepts. In these cases, the group responsible for the significant interaction was excluded from the ANCOVA model, and, subsequently, the effect of categorical predictor was tested across groups with statistically homogenous slopes, and their differences were compared based on differences in the intercepts. The planned comparisons of least-squares means was used to examine significant pairwise differences. To compare relative brain size between corvid and noncorvid songbirds, we computed t test on the residuals of a log-log regression of brain mass against body mass (residual brain mass, hereafter). For the comparison with cellular scaling rules reported previously for mammals, the reduced major axis regressions were calculated from quantitative data published for primates (33, 37, 38), rodents excluding the naked mole-rat (32,

39), and artiodactyls (36). In addition, the published quantitative data for Eulipothyphla (34) and Afrotheria (35) were used for comparison in Fig. S4.

The regressions were calculated using RMA for JAVA 1.21 (63); ANCOVA and t test, using Statistica 10.0 (Stat Soft); and all other analyses were performed in JMP 10.0 (SAS Institute).

SI Results

The results of the ANCOVA are summarized below for selected, important comparisons among taxonomic orders and brain regions. They are listed in order, in which they appear in the figures. *Ad Fig. 1.* (*B*) Allometric lines for songbirds (green line) and parrots (red line) do not differ from each other [full-factorial ANCOVA, slopes: $F_{(1,20)} = 0.537$, P = 0.47; intercepts: $F_{(1,20)} = 0.580$, P = 0.46], but they do differ from allometric lines for mammals [slopes: $F_{(4,40)} = 4.290$, P = 0.006; intercepts: $F_{(4,40)} = 3.595$, P = 0.014; post hoc analyses indicate that the regression line for rodents has a different slope and that parrots and songbirds have significantly smaller brains for a given number of neurons than primates and artiodactyls, $P < 10^{-6}$ for all planned comparisons].

(*E*) Allometric lines for the taxa examined are significantly different [slopes: $F_{(5,38)} = 3.653$, P = 0.009; intercepts: $F_{(5,38)} = 2.558$, P = 0.043; post hoc analyses indicate that the regression line for primates has a different slope and that parrots and songbirds have a significantly higher number of neurons for a given body mass than rodents and artiodactyls, P < 0.001 for all planned comparisons].

Ad Fig. 2. (*B* and *C*) Neuronal density varies significantly among principal brain divisions in both parrots [slopes: $F_{(4,45)} = 16.2, P < 10^{-6}$; intercepts: $F_{(4,45)} = 233.0, P < 10^{-6}$] and songbirds [slopes: $F_{(4,55)} = 14.4, P < 10^{-6}$; intercepts: $F_{(4,55)} = 523.9, P < 10^{-6}$].

(*D* and *E*) Comparison of the telencephalon with data pooled for the all other structures examined indicate that nonneuronal cell density is significantly lower in the telencephalon than in the remaining brain divisions in both parrots [slopes: $F_{(1,51)} = 0.00$, P = 0.995; intercepts: $F_{(1,51)} = 58.94$, $P < 10^{-6}$] and songbirds [slopes: $F_{(1,61)} = 0.0$, P = 0.838; intercepts: $F_{(1,61)} = 238.0$, $P < 10^{-6}$]. *Ad Fig. 3.* (*A*) Pallial neuronal densities are significantly higher in parrots and songbirds than in mammals [slopes: $F_{(4,41)} = 5.948$, P = 0.0007; intercepts: $F_{(4,41)} = 75.688$, $P = < 10^{-6}$; post hoc analyses indicate that the regression line for rodents has a different slope and that parrots and songbirds have significantly higher telencephalic neuronal densities than primates and artiodactyls, $P < 10^{-6}$ for all planned comparisons].

(*B*) Cerebellar neuronal densities tend to be higher in parrots and songbirds than in mammals [slopes: $F_{(4,40)} = 7.84$, $P < 10^{-4}$; intercepts: $F_{(4,40)} = 24.71$, $P = < 10^{-6}$; post hoc analyses indicate that the regression line for primates has a different slope and that parrots and songbirds have significantly higher cerebellar neuronal densities than rodents and artiodactyls, $P < 10^{-4}$ for all planned comparisons].

(*C*) Neuronal densities in the rest of brain are significantly higher in parrots and songbirds than in mammals [slopes: $F_{(4,41)} = 4.876$, P = 0.003; intercepts: $F_{(4,41)} = 86.875$, $P = < 10^{-6}$; post hoc analyses indicate that the regression line for parrots and for rodents differ in slope from other regression lines and that songbirds have significantly higher neuronal densities than primates and artiodactyls, $P < 10^{-6}$ for all planned comparisons].

Ad Fig. 5. (C) Allometric lines for songbirds (green line) and parrots (red line) differ significantly in slope $[F_{(1,20)} = 17.232, P = 0.0005]$.



Fig. S1. Phylogenetic relationships among the 28 species examined. The tree was constructed using birdtree.org/; its topology follows recent studies (46–49). Note that songbirds and parrots are sister groups and together with the distantly related barn owl belong to the clade core landbirds (Telluraves); the pigeon represents the Columbea, a basal clade of the Neoaves; the red junglefowl represents the Galloanseres, a sister group of Neoaves and the most basal clade of Neognathae; and the emu represents Paleognathae (tinamous and flightless ostriches), the most basal clade of extant birds (48). Also note that all passerine birds examined were vocal learners belonging to the clade Oscines.



Fig. 52. Brain dissection and labeling of neurons and nonneuronal cells. (*A* and *B*) Brain of the raven before and after the dissection. (*A*) Ventral side of the brain showing approximate lines of dissection of the brainstem and tectum. (*B*) Brain dissected into parts used for isotropic fractionation. (*C*) NeuN-immunolabeled transverse section of the zebra finch brain depicting the line of dissection of the tectum from the rest of the mesencephalon. (*D*–*F*) Dissection of the telencephalon into pallium and subpallium. NeuN-immunolabeled transverse sections of the zebra finch brain at outpallial-subpallial lamina and divide the telencephalon into pallium (dorsal part) and subpallium (ventral part). Coordinates anterior to the Y point are indicated in millimeters at *Bottom Left* (64). (*G*–*I*) High-power micrographs showing a sample of homogenate from the telencephalon of the Eurasian jay; dissociated nuclei stained with DAPI (*G*) and immunolabeled with NeuN antibody (*H*), dual-fluorescence merge image (*J*). Note that neurons are double-labeled, whereas the nonneuronal cells are devoid of anti-NeuN immunoreactivity. [Scale bars: 10 mm (*A* and *B*); 1 mm (*C* and *F*); 50 µm (*J*).]



Fig. S3. Brain size, morphology, and number of neurons for the avian species examined. Dorsal and lateral views of representative brains are accompanied by information concerning total number of brain neurons (yellow), number of pallial neurons (blue), and brain mass (red). M, million. (Scale bar, 10 mm.)

S A Z d



Fig. 54. Brain-body scaling in birds and mammals. (*A* and *B*) Taxonomic differences in relative brain size among songbirds (including both Oscines and Suboscines), parrots, primates, and nonprimate mammals. *Inset* in *A* corresponds to the magnified view shown in *B*. Note that allometric lines for these taxonomic groups are significantly different [full-factorial ANCOVA, slopes: $F_{(3,2618)} = 78.43$, $P < 10^{-6}$; intercepts: $F_{(3,2618)} = 7.44$, $P < 10^{-4}$; post hoc analyses indicate that the regression line for primates has a different slope (P < 0.001 for all pairwise comparisons) and that parrots and songbirds have significantly larger brains for a given body mass than nonprimate mammals ($P < 10^{-6}$ for both planned comparisons)]. (C) Relative brain size differences among parrots, corvids, and noncorvid songbirds. Note that allometric lines for these taxonomic groups are significantly different [slopes: $F_{(2,996)} = 4.24$, P = 0.014; intercepts: $F_{(2,996)} = 5.99$, P = 0.003; post hoc analyses indicate the regression line for songbirds has a different slope (P < 0.045 for both planned comparisons)]. (C) Relative brain size differences among parrots, corvids, and noncorvid songbirds. Note that allometric lines for these taxonomic groups are significantly different [slopes: $F_{(2,996)} = 4.24$, P = 0.014; intercepts: $F_{(2,996)} = 5.99$, P = 0.003; post hoc analyses indicate the regression line for songbirds has a different slope ($P \le 0.045$ for both planned comparisons) and that parrots have significantly larger brains for a given body mass than corvids ($P < 10^{-6}$]. Mean brain mass versus mean body mass for species are plotted; the fitted lines represent reduced major axis regressions. The relationship between brain mass and body mass can be described by the following power functions: songbirds, $M_{BR} = 0.087 \times M_{BO}^{0.737}$, $r^2 = 0.953$; noncorvid songbirds, $M_{BR} = 0.096 \times M_{BO}^{0.698}$, $r^2 = 0.92$; corvids, $M_{BR} = 0.097 \times M_{BO}^{0.725}$, $r^2 = 0.95$

Ordered by

Rank Body mass (g) Body mass (g) African elephapt $(4x10^6)$ Giraffe $(4.7x10^5)$ Greater kudu $(2.2x10^5)$ Pig $(1x10^5)$ Human $(7x10^4)$ Damaliscus $(6x10^4)$ Capybara $(4.8x10^4)$ Emu $(3.3x10^4)$ Springbok $(2.5x10^4)$ Bonnet monkey (8,013)Baboon (8,000)Long-tailed macaque (5,700)Rabbit (4,600)Rhesus monkey (3,900)Capuchin monkey (3,900)Capuchin monkey (3,340)Agouti (2,843)Rock hyrax (2,517)Prairie dog(1,515)Western tree hyrax (1,150)Raven (1,070)Blue&Yellow Macaw (1,008)Galago (946.7)Owl monkey (925.0)Red Junglefowl (861.3)Squirrel monkey (858.8)Kea (708.0)123456789012345678901234567890123456789001234567890112345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345 Red Junglerowi (851.3) Squirrel monkey (858.8) Kea (708.0) Squirrel (500.0) Grey Parrot (453.5) Sulphur-Cr. Cockatoo (430.0) Rook (429.3) Barn Owi (369.7) Marmoset (361.0) Marmoset (361.0) Rock Pigeon (322.5) Rock Pigeon (322.5) Rat (315.1) Guinea pig (311.0) Hill Mynah (262.1) Goffin's cockatoo (244.8) Proechimys (223.5) Alexandrine Parakeet (223.0) Jackdaw (209.7) Magpie (178.6) Tree shrew (172.5) Hamster (168.1) Eurasian Jay (160.0) Four-toed elep. shrew (132.5) Eastern Rosella (102.0) Cockatiel (101.0) Eastern mole (95.30) Eastern mole (95.30) Monk Parakeet (93.96) Blackbird (85.02) Azure-Winged Magpie (84.11) Golden mole (79.00) Starling (73.07) Mouse lemur (60.00) Elephant shrew (45.08) Hairy-tailed mole (41.40) Starnosed mole (41.40) ole (à Star-nosed mole (41.40) Mouse (40.40) Budgerigar (35.33) Green-Rump. Parrotlet (23.23) Zebra Finch (17.39) Great Tit (17.12) Blackcap (16.58) Short-tailed shrew (16.16) Carole actions (7.77) 65 66 Goldcrest (4.52)

Brain mass (g) African elephant (4,661) Human (1,509) Giraffe (539) Greater kudu (314) Giraffe (539) Greater kudu (314) Damaliscus (155) Baboon (151) Springbok (107) Rhesus monkey (87.4) Capybara (76.0) Pig (65.0) Bonnet monkey (61.5) Capuchin monkey (52.2) Long-tailed macaque (46.2) Squirrel monkey (30.2) Emu (21.8) Blue&Yellow Macaw (20.7) Agouti (18.4) Rock hyrax (17.1) Owl monkey (15.8) Raven (14.1) Kea (13.6) Western tree hyrax (12.8) Galago (10.2) Sulphur-Cr. Cockatoo (10.1) Rabbit (9.29) Grey Parrot (8.83) Rook (8.36) Goffin's cockatoo (8.27) Marmoset (7.79) Jackdaw (6.02) Jackdaw (6.02) Squirrel (5.76) Alexandrine Pa arakeet (5.69) Alexandrine Parakeet (3.09) Barn Owi (5.62) Magpie (5.43) Prairie dog (5.32) Eurasian Jay (4.59) Guinea pig (3.76) Hill Mynah (3.67) Monk Parakeet (3.42) Azure-Winged Magpie (3.39) Tree shrew (2.85) Red Junglefowi (2.82) Eastern Rosella (2.72) Four-toed elep. shrew (2.60) Cockatiel (2.21) Proechimys (2.21) Rock Pigeon (2.10) Blackbird (1.89) Starling (1.86) Mouse lemur (1.83) Rat (1.80) Budgerigar (1.32) Green-Rump. Parrotlet (1.15) Eastern mole (1.15) Barn Owl (5.62) Elephant shrew (1.09) Hamster (1.02) Great Tit (0.94 Golden mole (0.86) 85 Blackcap (0.77) Zebra Finch (0.49) Mouse (0.42) rew (0.37) Goldcrest (0.36) Smoky shrew (0.19)

Brain neurons (x10⁶) Brain neurons (x10°) African elephant (257,951) Human (86,060) Baboon (10,950) Giraffe (10,775) Rhesus monkey (6,391) Greater kudu (4,948) Bonnet monkey (3,780) Capuchin monkey (3,691) Long-tailed macaque (3,439) Squirrel monkey (3,246) Blue&Yellow Macaw (3,136) Damaliscus (3,060) Springbok (2,736) Pig (2,229) Raven (2,171) Kea (2,149) Sulphur-Cr. Cockatoo (2,122) Capybara (1,601) Grey Parrot (1,566) Rook (1,509) Owl monkey (1,478) Rook (1,509) Owl monkey (1,478) Emu (1,335) Goffin's cockatoo (1,161) Alexandrine Parakeet (1,096) Eurasian Jay (1,085) Jackdaw (968) Galago (936) Hill Mynah (906) Magpie (897) Rock hyrax (777) Agouti (753) Azure-Winged Magpie (741) Monk Parakeet (697) Barn Owl (690) Eastern Rosella (642) Eastern Rosella (642) Marmoset (638) Rabbit (513) Western tree hyrax (505) Starling (483) Squirrel (479) Prairie dog (474) Blackbird (379) Budgerigar (322) Rock Pigeon (310) Tree shrew (274) Mouse lemur (262) Guinea pig (240) Eastern mole (238) Green-Rump. Parrotlet (227) Great Tit (226) Red Junglefowl (221) Proechimys (211) Rat (200) Four-toed eleph. shrew (170) Goldcrest (164) Blackcap (157) Star-nosed mole (142) mole Elephant shrew (139) Elephant shrew (139) Zebra Finch (136) Hamster (90.0) Mouse (70.9) Golden mole (67.1) Short-tailed shrew (58.8) Smoky shrew (39.49)

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Pallium neurons (x10⁶)

Human (16,340) African elephant (5,593) Baboon (2,880) Blue&Yellow Macaw (1,917) Giraffe (1,730) Rhesus monkey (1,710) Bonnet monkey (1,660) Squirrel monkey (1,340) Kea (1,281) Raven (1,204) Capuchin monkey (1,140) Sulphur-Cr. Cockatoo (1,135) Grey Parrot (850) Rook (820) Long-tailed macaque (801) Greater kudu (763) Goffin's cockatoo (599) Alexandrine Parakeet (575) Damaliscus (571) Eurasian Jay (529) Jackdaw (492) Magpie (443) Owl monkey (442) Emu (439) Barn Owl (437) Human (16,340) Magpie (443) Owi monkey (442) Emu (439) Barn Owi (437) Hill Mynah (410) Azure-Winged Magpie (400) Springbok (397) Monk Parakeet (396) Eastern Rosella (333) Pig (307) Capybara (307) Cockatiel (258) Marmoset (245) Starling (226) Galago (226) Rock hyrax (198) Budgerigar (149) Blackbird (136) Agouti (111) Green-Rump. Parrotlet (103) Western tree hyrax (99.0) Great Tit (82.0) Western tree hyrax (99.0) Great Tit (83.0) Squirrel (77.3) Rock Pigeon (71.9) Rabbit (71.5) Goldcrest (64.2) Goldcrest (64.2) Red Junglefowl (60.7) Tree shrew (60.4) Zebra Finch (55.2) Prairie dog (53.8) Blackcap (52.2) Guinea pig (43.5) Four-toed eleph. shrew (33.9) Rat (31.0) Fastern mole (28.7) Proechimys (26.1) Elephant shrew (25.9) Mouse lemur (22.3) Golden mole (21.5) le (17.3) Hamster (17.1) Hamster (17.1) Hairy-tailed mole (15.7) Short-tailed shrew (15.4) Mouse (13.7) Smoky shrew (9.73)

E	ots 9birds Jates ents 2dactyli theria Potyph
	Part Son Artic Afr Euli
Body mass	39 50 15 31 4 32 57
Brain mass	32 40 13 36 5 33 60
Brain neurons	24 32 9 45 12 47 59
Pallium neurons	18 27 11 52 19 48 63

Fig. S5. Quantitative data currently available for the avian and mammalian species examined with the isotropic fractionator. (*A–D*) Species ranked in descending order from the largest to the smallest body mass (*A*), brain mass (*B*), total number of brain neurons (*C*), and total number of pallial neurons (*D*). The mean values of these variables are given in brackets. (*E*) Median ranks for the avian and mammalian clades examined. Data for mammals are from published reports (32–39).



Songbirds, Parrots, Pigeon (CL), Red junglefowl (GG), Barn owl (TA), Emu (DN).

Fig. S6. Glia/neuron ratios for the avian species examined. Each point represents the average proportion of nonneuronal cells (left axis) and the glia/neuron ratio (right axis) for one species, plotted against the average brain mass for that species. Songbirds are shown in green, parrots in red, and other birds in black. (*A*) The overall glia/neuron ratio in the brain. Note the higher proportion of nonneuronal cells in all outgroup taxa. (*B*) Variation in the glia/neuron ratio among the principal brain divisions investigated. Note that nonneuronal cells constitute a minor cellular fraction in the telencephalon of all species except three representatives of basal bird lineages—the emu, the red junglefowl, and the pigeon. Also note the high proportion of nonneuronal cells in the brainstem and the diencephalon.

•					
Species		Body mass, g	Brain mass, g	Total neurons, $\times 10^6$	Total nonneurons, ×10 ⁶
Parrots					
Green-rumped parrotlet	3	23.2 ± 0.7	1.146 ± 0.042	227.20 ± 3.81	135.00 ± 4.70
Budgerigar	3	35.3 ± 4.6	1.317 ± 0.041	321.82 ± 10.62	176.05 ± 4.26
Cockatiel	3	101.0 ± 4.6	2.205 ± 0.132	452.77 ± 44.51	234.66 ± 10.25
Eastern rosella	3	102.0 ± 3.4	2.716 ± 0.032	641.88 ± 79.00	318.17 ± 47.28
Monk parakeet	3	94.0 ± 1.7	3.420 ± 0.168	696.77 ± 75.26	393.49 ± 21.06
Alexandrine parakeet	3	223.0 ± 5.3	5.699 ± 0.492	1,096.26 ± 89.81	572.74 ± 28.11
Goffin's cockatoo	2	244.8 ± 3.5	8.275 ± 0.548	1,160.59 ± 101.87	792.22 ± 39.88
Gray parrot	2	453.5 ± 47.4	8.827 ± 0.859	1,565.93 ± 128.99	880.59 ± 2.06
Sulfur-crested cockatoo	1	430.0	10.131	2,121.93	1,001.81
Kea	1	708.0	13.593	2,148.67	975.57
Blue and yellow macaw	1	1,008.0	20.731	3,135.79	1,800.03
Variation, max./min.		43.3×	18.1×	13.8×	13.3×
Songbirds					
Goldcrest	3	4.5 ± 0.1	0.357 ± 0.022	163.87 ± 8.67	44.16 ± 6.57
Zebra finch	3	17.4 ± 2.1	0.494 ± 0.040	135.98 ± 6.82	59.75 ± 2.03
Blackcap	3	16.6 ± 1.3	0.774 ± 0.037	156.73 ± 18.91	86.28 ± 9.18
Great tit	3	17.1 ± 0.3	0.940 ± 0.066	225.98 ± 46.97	115.43 ± 23.43
Starling	3	73.1 ± 1.9	1.855 ± 0.047	482.50 ± 88.29	215.64 ± 13.49
Blackbird	3	85.0 ± 7.5	1.887 ± 0.117	379.41 ± 43.33	222.57 ± 27.48
Azure-winged magpie	2	84.1 ± 16.0	3.393 ± 0.486	740.59 ± 0.35	349.49 ± 33.17
Hill mynah	2	262.1 ± 30.7	3.670 ± 0.362	906.13 ± 45.38	380.79 ± 3.56
Eurasian jay	3	160.0 ± 12.5	4.597 ± 0.307	1,085.42 ± 159.56	484.42 ± 32.87
Magpie	3	178.6 ± 11.5	5.425 ± 0.617	897.27 ± 57.43	535.97 ± 15.96
Jackdaw	3	209.7 ± 25.1	6.023 ± 0.305	967.99 ± 106.66	565.92 ± 37.87
Rook	3	429.3 ± 35.6	8.357 ± 0.312	1,508.72 ± 38.25	855.55 ± 92.10
Raven	3	1,070.7 ± 73.2	14.135 ± 0.558	2,170.68 ± 72.67	1,242.85 ± 98.19
Variation, max./min.		237.9×	39.6×	16×	28.1×
Other birds					
Rock pigeon	3	322.5 ± 22.7	2.095 ± 0.123	309.96 ± 33.33	262.18 ± 18.94
Red junglefowl	3	861.3 ± 107.3	2.819 ± 0.200	220.84 ± 44.50	286.68 ± 17.35
Barn owl	3	369.7 ± 37.7	5.618 ± 0.404	689.54 ± 39.64	522.49 ± 25.29
Emu	2	32,600.0 ± 1,414.2	21.811 ± 2.037	1,335.40 ± 29.01	1,528.66 ± 118.97

Table S1. Cellular composition of the brains of 28 bird species

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Species ordered by increasing brain size. All values are given as mean \pm SD; *n*, number of individuals analyzed.

Table S2.	Cellular scaling	rules for	brains of	parrots and	songbirds

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Dependent variable	Independent variable	Power law	r ²	P value (exponent)	95% confidence interval
Parrots					
M _{BR}	N _{BR}	$M_{BR} = 2.669 \times 10^{-10} \times N_{BR}^{1.144}$	0.979	<0.000 1	1.020–1.269
M _{TEL}	N _{TEL}	$M_{TEL} = 1.356 \times 10^{-9} \times N_{TEL}^{1.075}$	0.967	<0.000 1	0.928-1.221
M _{DIE}	N _{DIE}	$M_{DIE} = 5.027 \times 10^{-15} \times N_{DIE}^{2.031}$	0.827	<0.000 1	1.395–2.668
M _{TEC}	N _{TEC}	$M_{TEC} = 5.492 \times 10^{-16} \times N_{TEC}^{1.998}$	0.945	<0.000 1	1.645-2.350
M _{CB}	N _{CB}	$M_{CB} = 3.030 \times 10^{-11} \times N_{CB}^{1.198}$	0.974	<0.000 1	1.052-1.344
M _{BS}	N _{BS}	$M_{BS} = 1.752 \times 10^{-20} \times N_{BS}^{2.968}$	0.911	<0.000 1	2.304-3.633
M _{BR}	O _{BR}	$M_{BR} = 3.267 \times 10^{-10} \times O_{BR}^{1.170}$	0.989	<0.000 1	1.076-1.263
M _{TEL}	O _{TEL}	$M_{TEL} = 9.805 \times 10^{-10} \times O_{TEL}^{1.126}$	0.991	<0.000 1	1.043-1.208
M _{DIE}	O _{DIE}	$M_{DIE} = 2.622 \times 10^{-17} \times O_{DIE}^{1.102}$	0.989	<0.000 1	1.015–1.189
M _{TEC}	O _{TEC}	$M_{TEC} = 3.822 \times 10^{-10} \times O_{TEC}^{1.160}$	0.938	<0.000 1	0.943-1.380
M _{CB}	O _{CB}	$M_{CB} = 2.440 \times 10^{-10} \times O_{CB}^{1.160}$	0.970	<0.000 1	1.031-1.343
M _{BS}	O _{BS}	$M_{BS} = 2.567 \times 10^{-10} \times O_{BS}^{-1.186}$	0.987	<0.000 1	1.081–1.288
Songbirds					
M _{BR}	N _{BR}	$M_{BR} = 4.699 \times 10^{-11} \times N_{BR}^{1.227}$	0.962	<0.000 1	1.068–1.387
M _{TEL}	N _{TEL}	$M_{TEL} = 4.678 \times 10^{-11} \times N_{TEL}^{1.134}$	0.940	<0.000 1	0.949-1.320
M _{DIE}	N _{DIE}	$M_{DIE} = 2.322 \times 10^{-16} \times N_{DIE}^{2.208}$	0.952	<0.000 1	1.882–2.520
M _{TEC}	N _{TEC}	$M_{TEC} = 2.024 \times 10^{-14} \times N_{TEC}^{1.736}$	0.934	<0.000 1	1.440-2.033
M _{CB}	N _{CB}	$M_{CB} = 2.013 \times 10^{-11} \times N_{CB}^{1.206}$	0.972	<0.000 1	1.072-1.340
M _{BS}	N _{BS}	$M_{BS} = 2.776 \times 10^{-17} \times N_{BS}^{2.445}$	0.950	<0.000 1	2.081-2.810
M _{BR}	O _{BR}	$M_{BR} = 1.536 \times 10^{-9} \times O_{BR}^{1.093}$	0.998	<0.000 1	1.060-1.125
M _{TEL}	O _{TEL}	$M_{TEL} = 5.399 \times 10^{-9} \times O_{TEL}^{1.043}$	0.997	<0.000 1	1.007–1.080
M _{DIE}	O _{DIE}	$M_{DIE} = 6.292 \times 10^{-9} \times O_{DIE}^{0.992}$	0.996	<0.000 1	0.953-1.032
M _{TEC}	O _{TEC}	$M_{TEC} = 1.465 \times 10^{-9} \times O_{TEC}^{0.946}$	0.994	<0.000 1	0.897–0.996
M _{CB}	O _{CB}	$M_{CB} = 2.102 \times 10^{-10} \times O_{CB}^{1.191}$	0.965	<0.000 1	1.043–1.339
M _{BS}	O _{BS}	$M_{BS} = 2.907 \times 10^{-9} \times O_{BS}^{1.040}$	0.993	<0.000 1	0.980-1.100

Power laws were calculated from the average species values listed in Tables S1 and S3–S5. BR, brain; BS, brainstem; CB, cerebellum; DIE, diencephalon; M, mass (in grams); N, number of neurons; O, number of other (nonneuronal) cells; r^2 , coefficient of determination calculated from the reduced major axis regression of species averages; TEC, tectum; TEL, telencephalon.

Table S3. Mass of the major brain divisions of 28 bird species

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Subpallium,								
Species	Telencephalon, g	% of Tel	Diencephalon, g	Tectum, g	Cerebellum, g	Brainstem, g		
Parrots								
Green-rumped parrotlet	0.851 ± 0.039	16.0	0.067 ± 0.003	0.066 ± 0.004	0.098 ± 0.002	0.064 ± 0.003		
Budgerigar	0.935 ± 0.039	17.1	0.078 ± 0.012	0.073 ± 0.002	0.144 ± 0.006	0.086 ± 0.005		
Cockatiel	1.617 ± 0.098	15.4	0.119 ± 0.006	0.136 ± 0.010	0.196 ± 0.011	0.138 ± 0.016		
Eastern rosella	2.009 ± 0.053	15.2	0.145 ± 0.002	0.175 ± 0.015	0.230 ± 0.017	0.156 ± 0.006		
Monk parakeet	2.663 ± 0.168	15.9	0.162 ± 0.008	0.150 ± 0.005	0.281 ± 0.002	0.165 ± 0.013		
Alexandrine parakeet	4.390 ± 0.412	16.7	0.292 ± 0.025	0.240 ± 0.009	0.506 ± 0.040	0.272 ± 0.013		
Goffin's cockatoo	6.689 ± 0.429	17.7	0.399 ± 0.045	0.288 ± 0.001	0.571 ± 0.034	0.328 ± 0.038		
Gray parrot	6.973 ± 0.780	14.8	0.431 ± 0.079	0.331 ± 0.035	0.638 ± 0.007	0.454 ± 0.028		
Sulfur-crested cockatoo	8.072	16.2	0.496	0.304	0.836	0.423		
Кеа	11.383	16.7	0.504	0.372	0.825	0.509		
Blue and yellow macaw	17.565	18.2	0.783	0.506	1.245	0.632		
Variation, max./min.	20.7×		11.7×	7.7×	12.7×	9.9×		
Songbirds								
Goldcrest	0.225 ± 0.023	22.0	0.024 ± 0.002	0.045 ± 0.004	0.040 ± 0.002	0.023 ± 0.002		
Zebra finch	0.327 ± 0.026	15.6	0.032 ± 0.006	0.043 ± 0.003	0.056 ± 0.009	0.036 ± 0.003		
Blackcap	0.516 ± 0.036	12.0	0.056 ± 0.002	0.071 ± 0.003	0.084 ± 0.002	0.047 ± 0.004		
Great tit	0.675 ± 0.051	14.0	0.056 ± 0.002	0.073 ± 0.008	0.090 ± 0.007	0.046 ± 0.004		
Starling	1.287 ± 0.018	11.2	0.113 ± 0.008	0.155 ± 0.015	0.193 ± 0.013	0.107 ± 0.011		
Blackbird	1.272 ± 0.120	14.2	0.125 ± 0.014	0.171 ± 0.007	0.213 ± 0.015	0.107 ± 0.009		
Azure-winged magpie	2.594 ± 0.401	14.5	0.171 ± 0.014	0.217 ± 0.020	0.271 ± 0.035	0.140 ± 0.018		
Hill mynah	2.577 ± 0.300	16.2	0.184 ± 0.007	0.323 ± 0.018	0.367 ± 0.015	0.218 ± 0.022		
Eurasian jay	3.360 ± 0.296	15.1	0.251 ± 0.009	0.369 ± 0.034	0.411 ± 0.013	0.205 ± 0.004		
Magpie	4.193 ± 0.520	11.4	0.263 ± 0.015	0.318 ± 0.035	0.453 ± 0.037	0.197 ± 0.021		
Jackdaw	4.705 ± 0.221	11.5	0.280 ± 0.022	0.339 ± 0.010	0.483 ± 0.043	0.216 ± 0.012		
Rook	6.648 ± 0.246	13.2	0.322 ± 0.013	0.425 ± 0.014	0.657 ± 0.036	0.306 ± 0.013		
Raven	11.307 ± 0.450	9.8	0.570 ± 0.086	0.623 ± 0.073	1.145 ± 0.116	0.49 ± 0.012		
Variation, max./min.	50.3×		23.7×	14.5×	28.6×	21.3×		
Other birds								
Rock pigeon	1.095 ± 0.090	16.5	0.190 ± 0.006	0.281 ± 0.016	0.332 ± 0.013	0.196 ± 0.014		
Red junglefowl	1.567 ± 0.162	14.8	0.245 ± 0.014	0.345 ± 0.022	0.369 ± 0.024	0.293 ± 0.010		
Barn owl	4.141 ± 0.328	7.0	0.347 ± 0.007	0.192 ± 0.006	0.510 ± 0.080	0.427 ± 0.011		
Emu	14.238 ± 1.515	8.8	1.218 ± 0.072	1.184 ± 0.152	3.399 ± 0.181	1.773 ± 0.116		

Species ordered by increasing brain size. All values are given as mean \pm SD.

Table S4. Number of neurons in the major brain divisions of 28 bird species

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Subpallium,								
Species	Telencephalon, ×10 ⁶	% of Tel	Diencephalon, ×10 ⁶	Tectum, ×10 ⁶	Cerebellum, $\times 10^{6}$	Brainstem, $\times 10^6$		
Parrots								
Green-rumped parrotlet	120.84 ± 4.68	14.4	3.25 ± 0.49	11.44 ± 1.04	89.62 ± 5.08	2.05 ± 0.21		
Budgerigar	186.00 ± 4.09	19.9	3.34 ± 0.16	11.72 ± 2.09	118.73 ± 8.31	2.03 ± 0.46		
Cockatiel	301.81 ± 40.57	14.4	3.64 ± 1.68	16.11 ± 1.11	129.15 ± 7.77	2.06 ± 0.76		
Eastern rosella	406.32 ± 77.24	18.0	4.30 ± 0.77	16.98 ± 2.62	211.98 ± 25.42	2.31 ± 0.49		
Monk parakeet	476.50 ± 73.49	16.9	4.78 ± 1.33	17.49 ± 0.76	195.53 ± 22.69	2.47 ± 0.44		
Alexandrine parakeet	703.96 ± 94.37	18.4	5.16 ± 0.96	22.95 ± 4.78	361.36 ± 10.29	2.84 ± 0.52		
Goffin's cockatoo	715.08 ± 95.62	16.2	6.63 ± 0.37	22.71 ± 2.02	413.10 ± 7.67	3.07 ± 0.24		
Gray parrot	1,147.54 ± 73.25	25.9	6.75 ± 2.71	20.90 ± 2.53	387.40 ± 51.18	3.35 ± 0.69		
Sulfur-crested cockatoo	1,490.59	23.8	12.05	27.06	588.41	3.82		
Kea	1,630.49	21.4	7.13	26.57	481.14	3.35		
Blue and yellow macaw	2,459.15	22.0	7.85	31.22	633.52	4.06		
Variation, max./min.	20.4×		2.4×	2.7×	7.1×	2×		
Songbirds								
Goldcrest	76.13 ± 5.77	15.7	2.73 ± 0.17	16.99 ± 1.39	66.78 ± 3.28	1.26 ± 0.10		
Zebra finch	64.66 ± 2.84	14.6	2.40 ± 0.42	10.62 ± 0.50	56.61 ± 9.84	1.69 ± 0.46		
Blackcap	59.71 ± 6.23	12.6	3.15 ± 0.24	15.34 ± 2.31	76.94 ± 13.02	1.58 ± 0.14		
Great tit	96.38 ± 27.43	13.9	3.47 ± 0.67	16.19 ± 0.91	108.27 ± 20.71	1.67 ± 0.52		
Starling	257.08 ± 66.07	12.0	4.00 ± 0.88	25.44 ± 0.54	193.74 ± 25.00	2.24 ± 0.58		
Blackbird	157.63 ± 13.12	13.6	4.26 ± 0.55	28.26 ± 3.53	186.73 ± 33.99	2.52 ± 0.034		
Azure-winged magpie	454.25 ± 36.08	12.0	4.99 ± 1.34	35.35 ± 0.60	243.49 ± 35.05	2.51 ± 0.65		
Hill mynah	484.29 ± 49.32	15.3	4.90 ± 0.22	47.97 ± 0.33	365.74 ± 4.07	3.22 ± 0.24		
Eurasian jay	600.49 ± 139.10	11.9	6.75 ± 0.66	45.95 ± 2.22	429.35 ± 28.75	2.88 ± 0.47		
Magpie	497.94 ± 26.98	11.0	6.83 ± 1.14	40.44 ± 2.80	349.25 ± 27.82	2.82 ± 0.14		
Jackdaw	541.37 ± 63.55	9.2	6.82 ± 1.55	40.94 ± 4.55	375.46 ± 41.89	3.39 ± 0.73		
Rook	917.85 ± 68.58	10.6	7.56 ± 1.48	42.72 ± 3.59	536.28 ± 29.31	4.30 ± 0.45		
Raven	1,355.34 ± 73.26	11.2	10.15 ± 2.99	47.65 ± 7.31	753.64 ± 27.34	3.90 ± 0.18		
Variation, max./min.	22.7×		4.2×	4.5×	13.3×	3.1×		
Other birds								
Rock pigeon	83.35 ± 20.53	13.8	2.81 ± 0.69	23.76 ± 2.69	197.72 ± 11.37	2.31 ± 0.31		
Red junglefowl	73.79 ± 2.46	17.8	4.02 ± 0.76	25.50 ± 3.26	114.45 ± 39.59	3.08 ± 0.57		
Barn owl	453.73 ± 13.53	3.6	7.54 ± 1.19	9.33 ± 1.22	214.31 ± 32.07	4.63 ± 0.68		
Emu	471.57 ± 3.54	6.8	10.22 ± 2.48	33.72 ± 3.74	814.61 ± 17.66	5.28 ± 1.60		

Species ordered by increasing brain size. All values are given as mean \pm SD.

Table S5.	Number of	f nonneuronal	cells in	the	brain	divisions	of 28	bird	species
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		Subpallium,				
Species	Telencephalon, $\times 10^{6}$	% of Tel	Diencephalon, ×10 ⁶	Tectum, ×10 ⁶	Cerebellum, $\times 10^{6}$	Brainstem, $\times 10^6$
Parrots						
Green-rumped parrotlet	83.01 ± 2.45	15.0	11.95 ± 1.05	12.42 ± 2.35	16.18 ± 0.21	11.45 ± 0.98
Budgerigar	103.22 ± 2.23	20.2	15.49 ± 3.29	13.92 ± 2.91	27.08 ± 4.59	16.35 ± 1.72
Cockatiel	142.78 ± 14.01	19.1	20.83 ± 2.14	19.45 ± 2.96	29.72 ± 4.78	21.88 ± 3.05
Eastern rosella	193.56 ± 40.48	15.3	27.47 ± 4.39	31.22 ± 0.85	38.96 ± 2.26	26.97 ± 4.38
Monk parakeet	259.75 ± 20.81	16.1	34.24 ± 0.53	24.40 ± 1.78	45.40 ± 2.50	29.70 ± 1.39
Alexandrine parakeet	353.72 ± 34.43	16.2	47.91 ± 5.07	47.38 ± 8.48	79.03 ± 7.98	44.70 ± 1.78
Goffin's cockatoo	544.50 ± 7.14	24.6	66.51 ± 9.81	48.00 ± 0.51	79.60 ± 15.59	53.60 ± 7.85
Gray parrot	602.93 ± 2.07	10.2	72.44 ± 5.46	51.88 ± 6.34	90.70 ± 2.96	62.63 ± 4.71
Sulfur-crested cockatoo	688.63	17.7	87.57	47.89	114.59	63.12
Кеа	721.18	19.6	73.85	40.18	78.33	62.03
Blue and yellow macaw	1,383.27	16.3	115.1	66.95	152.48	82.23
Variation, max./min.	16.7×		9.6×	5.4×	9.4×	7.2×
Songbirds						
Goldcrest	20.48 ± 5.03	21.6	4.09 ± 0.75	6.69 ± 0.19	8.85 ± 1.62	4.05 ± 0.37
Zebra finch	28.89 ± 1.23	19.5	5.45 ± 1.06	7.13 ± 0.99	10.79 ± 2.49	7.49 ± 0.92
Blackcap	39.8 ± 3.12	11.5	9.79 ± 0.79	12.08 ± 2.93	16.19 ± 2.57	8.41 ± 0.40
Great tit	60.11 ± 18.23	17.1	10.29 ± 1.75	11.20 ± 0.77	25.94 ± 5.47	7.90 ± 1.12
Starling	115.05 ± 8.09	14.6	21.84 ± 1.57	26.31 ± 1.42	33.68 ± 5.78	18.76 ± 1.34
Blackbird	106.02 ± 16.65	18.2	23.54 ± 0.36	31.18 ± 3.71	42.11 ± 8.19	19.72 ± 0.81
Azure-winged magpie	220.70 ± 14.36	15.9	29.20 ± 9.40	38.51 ± 4.45	37.46 ± 0.75	23.62 ± 5.70
Hill mynah	199.22 ± 8.05	18.6	36.30 ± 3.52	58.41 ± 1.74	51.85 ± 0.90	35.00 ± 0.12
Eurasian jay	282.53 ± 34.69	16.1	47.84 ± 3.71	59.62 ± 7.81	59.59 ± 12.83	34.83 ± 3.65
Magpie	316.64 ± 9.68	11.6	50.33 ± 5.41	66.29 ± 3.52	64.73 ± 8.41	37.99 ± 1.72
Jackdaw	366.72 ± 40.30	13.5	51.35 ± 6.03	54.36 ± 1.95	57.82 ± 3.60	35.67 ± 1.47
Rook	562.20 ± 79.47	14.6	54.05 ± 3.73	79.57 ± 10.68	102.14 ± 13.90	57.59 ± 9.50
Raven	790.64 ± 80.16	12.2	94.86 ± 13.90	110.13 ± 22.37	173.96 ± 4.03	73.27 ± 3.51
Variation, max./min.	38.6×		23.2×	16.5×	19.7×	18.1×
Other birds						
Rock pigeon	102.02 ± 16.85	17.6	36.85 ± 1.58	41.55 ± 0.74	47.61 ± 3.58	34.16 ± 5.04
Red junglefowl	131.98 ± 9.48	17.0	38.42 ± 4.70	45.39 ± 7.09	28.28 ± 9.67	42.63 ± 0.98
Barn owl	339.01 ± 16.56	8.2	49.74 ± 4.50	25.39 ± 2.60	54.52 ± 10.61	53.82 ± 7.26
Emu	865.37 ± 74.72	11.2	124.24 ± 10.16	123.63 ± 16.28	231.05 ± 2.58	184.36 ± 20.40

Species ordered by increasing brain size. All values are given as mean \pm SD.

Other Supporting Information Files

Dataset S1 (XLSX) Dataset S2 (XLSX) Dataset S3 (DOCX)

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